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The morphology of *Ganoderma* species with a laccate surface

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Abstract — A discussion on the importance of morphological features in the taxonomy of *Ganoderma* subg. *Ganoderma* is presented. More than 500 specimens of 37 species, including 33 types, were checked: *G. argillaceum*, *G. atkinsonii*, *G. boninense*, *G. capense*, *G. chonoides*, *G. colossus*, *G. concinnum*, *G. corrugatum*, *G. curtisii*, *G. dorsale*, *G. elegantum*, *G. longistipitatum*, *G. mexicanum*, *G. multicornum*, *G. multiplicatum*, *G. nevadense*, *G. nitidum*, *G. oerstedii*, *G. orbiforme*, *G. oregonense*, *G. parvulum*, *G. perturbatum*, *G. perzonatum*, *G. praelongum*, *G. pulverulentum*, *G. ravenelii*, *G. resinaceum*, *G. sequoiae*, *G. sessile*, *G. sessiliforme*, *G. simulans*, *G. stipitatum*, *G. subfornicatum*, *G. subincrustatum*, *G. vivianimercedianum*, *G. weberianum*, and *G. zonatum*. Color of the context, resinous deposits, structure of the basidiospores, and protuberances of the pileipellis cells are among the most important features for characterization of the species.

Key words — *Basidiomycota*, *Ganodermataceae*

Introduction

Ganoderma P. Karst. is characterized by its double-walled, colored basidiospores with a truncate or subacute apex and ornamented exosporium. The genus includes species with both dull [subg. *Elfvingia* (P. Karst.) Imazeki] and laccate pilei (subg. *Ganoderma*). The pileipellis has been differently characterized by different authors: (1) Furtado (1965a) refers to a derm of the palisadoderm type in *Elfvingia* and layer of cells in a hymeniderm in *Ganoderma,* while Steyaert (1980) refers to a trichoderm in *Elfvingia* and "hymenioderm" in subg. *Ganoderma*. Clémençon (2004) used "crustohymeniderm" for subg. *Ganoderma*, so following his definition, the *Elfvingia* pileipellis is a crustotrichoderm, because it is also incrusted with a resinous matter. Although phylogenetic analyses (Moncalvo 2000, Hong & Jung 2004) support the

monophyly of *Ganoderma* and its classification in two subgenera, there are many problems in the resolution below subgeneric level.

The micromorphological structures of some species or groups in *Ganoderma* have been studied by, among others, Patouillard (1889), Murrill (1902), Haddow (1931), Heim (1962), Furtado (1965a,b, 1967), Steyaert (1967a,b, 1972, 1975, 1977), Pegler & Young (1973), Corner (1983), and Adaskaveg & Gilbertson (1988). More recently, Gottlieb & Wright (1999) made a detailed study of the basidiospores under the Scanning Electron Microscope (SEM) in an attempt to solve some of the inter-specific problems. However, these studies have been restricted to a rather limited number of species and few used the pileipellis cells as a critical character in their species concepts.

Through the study of more than 500 specimens (including 33 types) mainly from Africa, Brazil, Costa Rica, Mexico, and USA, we analyzed the morphological variation of structures in *Ganoderma* subg. *Ganoderma* with the following aims: 1) to study in detail structures currently and potentially useful in taxonomy and phylogenetic analyses and 2) to probe the utility of light microscopy in defining basidiospore pillars.

Materials & methods

Specimens examined

More than 500 specimens from the herbaria BPI, BR, ENCB, FH, H, IBUG (including collections by the first author), INB, K, NY, O, PC, SP, UPS, and XAL were examined (acronyms follow Holmgren et al. 1990). These specimens comprised 37 species, which are listed in Table 1, which includes one representative specimen for each species.

Macro and micromorphological observations and identification

The following macromorphological characters were described for each basidiome: length, width, thickness, adhesion to the substrate, general shape, consistency, weight; pileus shape, surface consistency, color; context thickness, stratification, color, resinous deposits; pore form, number per mm, consistency, color; tube length, stratification, color. Macrochemical reactions used 10% KOH. In addition to the traditional microcharacters, descriptions include: basidiospore apex, disposition and size of basidiospore pillars, and pileipellis cell size, shape, and incrustations. Color references follow Kornerup & Wanscher (1963). Microscopical observations were made from basidioma tissues mounted in 10% KOH and Melzer's reagent, with Congo red, phloxine, and cotton blue additionally used. Basidiospore shape is determined from the Q ratio (l/b; Bas 1969: 320–321) of 20 randomly selected basidiospores. Only mature pileipellis cells were described. Microscopical observations were made using a 100× oil-immersion objective in Zeiss K7 and Zeiss Axioskop 40 microscopes. The inter-walled basidiospore pillars were measured using Axio Vision 4 software with the Zeiss Axioskop 40 microscope. Most morphological terms follow Vellinga (1998), Furtado (1965a), and Clémençon (2004). The pileipellis description follows the concepts of Clémençon (2004).

Table 1. Species of *Ganoderma* subg. *Ganoderma* with representative collections.

Species	Specimen
G. argillaceum Murrill	F.S. Earle 658 (lectotype, NY)
G. atkinsonii H. Jahn et al.	without data (O)
G. boninense Pat.	C. Wright s.n. (lectotype, K)
G. capense (Lloyd) Teng	P. van der Bijl s.n. (lectotype, NY)
G. chonoides Steyaert	without data (holotype, BR)
G. colossus (Fr.) C.F. Baker	A.S. Oersted s.n. (lectotype, UPS)
G. concinnum Ryvarden	L. Ryvarden 16840 (holotype, O)
G. corrugatum Steyaert	R.L. Steyaert 45061 (holotype, BR)
G. curtisii (Berk.) Murrill	P.O. Schallert s.n. (F1119720)
G. dorsale (Lloyd) Torrend	R.J. Rick s.n. (holotype, BPI)
G. elegantum Ryvarden	Ryvarden 44573 (holotype, O)
G. longistipitatum Ryvarden	L. Ryvarden 40588 (holotype, O)
G. mexicanum Pat.	without data (lectotype, FH)
G. multicornum Ryvarden	G.J. Samuels s.n. (holotype, O)
G. multiplicatum (Mont.) Pat.	R. Maziero s.n. (SP250605)
G. nevadense Murrill	C.F. Baker 1489 (lectotype, NY)
G. nitidum Murrill	P. Wilson 607 (lectotype, NY)
G. oerstedii (Fr.) Murrill	A.S. Oersted s.n. (neotype, UPS)
G. orbiforme (Fr.) Ryvarden	A. Afzelius s.n. (holotype, UPS)
G. oregonense Murrill	J.E. Kirkwood s.n. (lectotype, NY)
G. parvulum Murrill	C.L. Smith s.n. (lectotype, NY)
G. perturbatum (Lloyd) Torrend	R. Rick s.n. (holotype, BPI)
G. perzonatum Murrill	F.S. Earle 309 (lectotype, UPS)
G. praelongum Murrill	F.S. Earle & W.A. Murrill 536 (lectotype, NY)
G. pulverulentum Murrill	W.E. Broadway s.n. (lectotype, NY)
G. ravenelii Steyaert	H.W. Ravenel 2936 (holotype, K)
G. resinaceum Boud.	J.L. Boudier s.n. (holotype, PC)
G. sequoiae Murrill	A. Eastwood 40 (lectotype, NY)
G. sessile Murrill	without data (lectotype, NY)
G. sessiliforme Murrill	E. & W.A. Murrill 392 (lectotype, NY)
G. simulans Wakef.	T.D. Maitland 556 (isotype, O)
G. stipitatum (Murrill) Murrill	C.L. Smith s.n. (lectotype, NY)
G. subfornicatum Murrill	M.E. Peck s.n. (lectotype, NY)
G. subincrustatum Murrill	F.S. Earle 176 (lectotype, NY)
G. vivianimercedianum M.G. Torres	E. Bastidas-Varela s.n. (holotype, ENCB)
G. weberianum (Bres. & Henn. ex Sacc.) Steyaert	A. Milanez & D. Altimari s.n. (SP61099)
G. zonatum Murrill	L.M. Underwood s.n. (lectotype, NY)

Specimens were generally determined after comparing with the type or types of related species, but the keys of Bazzalo & Wright (1982) and Ryvarden (2004) and the descriptions of Steyaert (1972) and Corner (1983) were also used.

Results

The features proposed here are discussed below and are being used to describe and key *Ganoderma* species from Brazil and Mexico (Torres-Torres et al., papers in preparation).

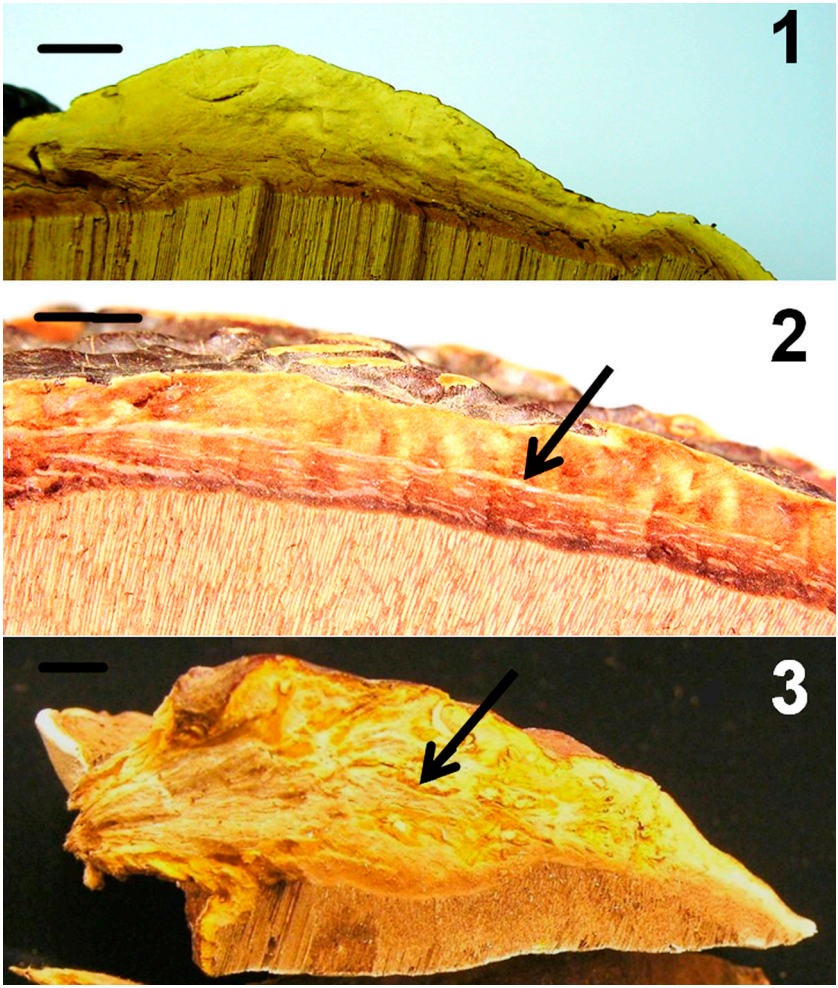
Macromorphological features

Basidiome shape and substrate attachment are of rather restricted value for taxon delimitation; however, basidiome consistency, weight, and thickness as well as the presence and attachment of the stipe proved, in some cases, to be valuable for identification. *Ganoderma atkinsonii*, *G. colossus*, *G. nevadense*, and *G. oregonense* have light, spongy basidiomata, while *G. zonatum* and *G. pulverulentum* have light, woody-corky basidiomata. *Ganoderma mexicanum*, *G. sessile*, *G. sessiliforme*, and *G. subincrustatum* have relatively light, woody basidiomata, while *Ganoderma oerstedii* has heavy, woody basidiomata. *Ganoderma colossus*, *G. oregonense*, *G. oerstedii*, *G. sessile*, and *G. zonatum* are generally robust, while *G. mexicanum*, *G. parvulum*, *G. sessiliforme*, and *G. weberianum* have slender basidiomata.

The more important features of the pileus context for diagnosing species are: (1) consistency, (2) structure, and (3) presence of resinous deposits. Only three types of context consistency are recognized. Two — soft-spongy and fibrous — are easy to distinguish, but there is an intermediate state between soft and fibrous that is difficult to identify. In this study, the third type was termed "fibrous-spongy." *Ganoderma colossus* and *G. oregonense* have soft-spongy context, *G. sessiliforme* has fibrous context, and *G. resinaceum* has fibrous-spongy context.

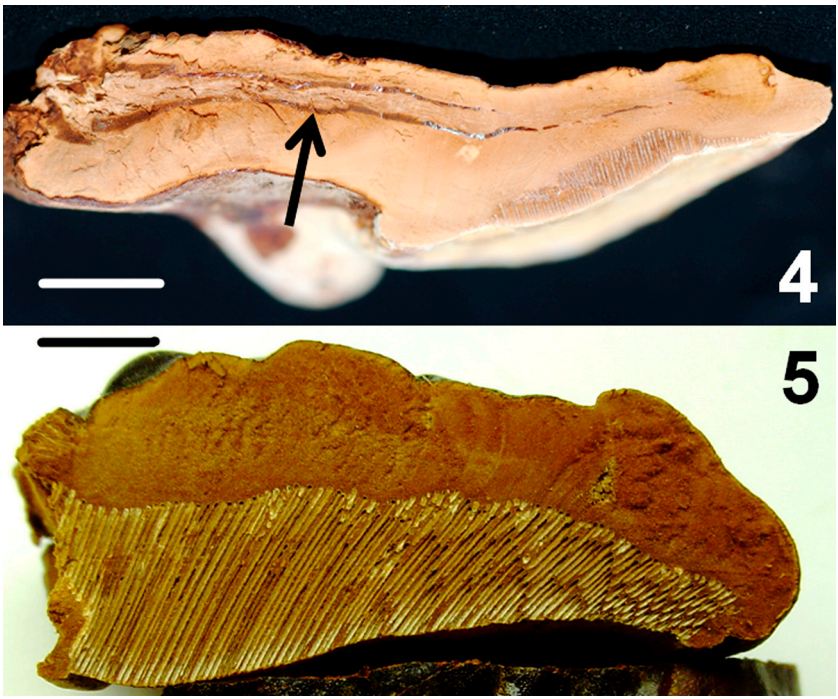
The context structure is classified as (1) duplex, (2) not fully homogeneous, or (3) homogeneous. In the duplex context there is an abrupt change, with two separate, contrasting colors, the upper generally light-colored and the lower generally darker close to the tubes, although shades may vary to some extent. This context type is present in *G. concinnum*, *G. curtisii*, *G. dorsale*, and *G. sessile* (Fig. 1). Not fully homogeneous is used when there is an evident color difference between the upper and lower parts but without abrupt color changes, like in *G. oerstedii* (Fig. 2), *G. perturbatum*, *G. perzonatum*, *G. weberianum* (Fig. 3), while a homogeneous context has only one color, as in *G. parvulum* and *G. resinaceum* (Figs. 4–5). Contexts with an occasional very thin darker line just above the tubes that is absent in some specimens are considered as homogeneous. The context can contain resin-like deposits (hard and brittle, dull or shiny) that often they form continuous bands (here "resinous bands," see *G. oerstedii* and *G. parvulum* in Figs. 2, 4) or discrete bodies (here "resinous incrustations," see *G. weberianum,* Fig. 3).

Some authors (Patouillard 1889, Moncalvo 2000, Seo & Kirk 2000) have dismissed the stipe as a character of no taxonomic value, because some sessile species can develop a stipe in the laboratory resulting from varying oxygen conditions. Nevertheless, the stipe is a useful character, with a "true" stipe defined as one > 5 cm and with tissues differentiated from the pileus context. Some species develop a generally short (<5 cm) pseudostipe that is merely a



Figs. 1–3. *Ganoderma* macromorphology. **1**. Duplex context *(G. sessile)*. **2**. Not completely homogeneous context *(G. oerstedii)*; continuous bands of the resin-like deposits (arrowed). **3**. Not completely homogeneous context *(G. weberianum)*; discrete bodies of the resin-like deposits (arrowed). Bar = 2 cm.

continuation of the pileus and which Steyaert (1980) termed a "pedicel" and we call a "substipe." Species such as *G. curtisii*, *G. concinnum*, *G. dorsale*, and *G. perturbatum* always present a true stipe, while *G. pulverulentum* and *G. weberianum* can develop a substipe dependent upon environmental and nutritional conditions.

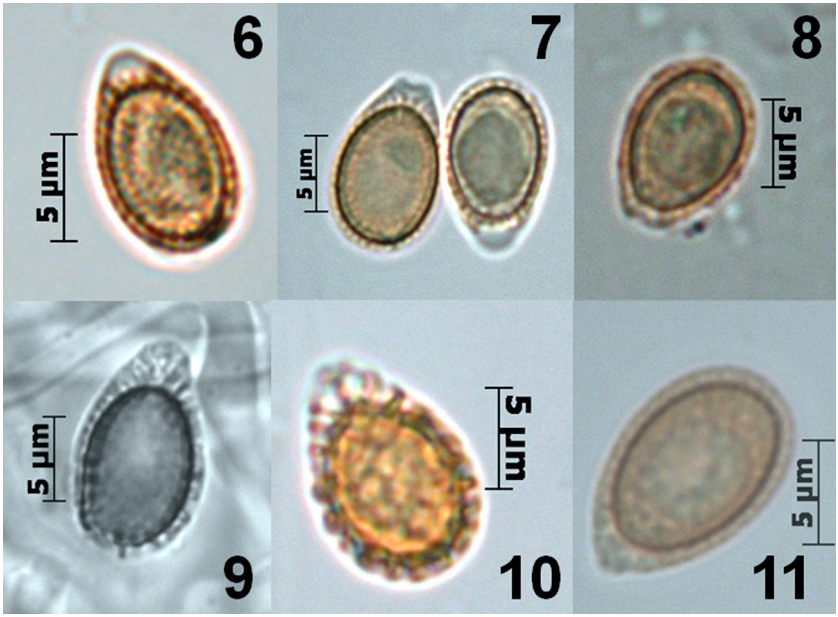


Figs. 4–5. *Ganoderma* macromorphology. **4**. Homogenous context *(G. parvulum)*; continuous bands of the resin-like deposits (arrowed). **5**. Homogeneous context *(G. resinaceum)*; note the absence of resin-like deposits. Bar = 2 cm.

Micromorphological features

Basidiospores. Following Clémençon's (2004) terminology, all *Ganoderma* basidiospores have a thin, smooth or rugose, hyaline to reddish-yellow perisporium; an ornamented colored exosporium with pillars, and a thick reddish-brown or yellowish-brown endosporium. Using the Q ratio categories (Bas 1969), most species have ellipsoid to elongate (= oblong) basidiospores, while *G. concinnum*, *G. dorsale* and *G. perturbatum* have distinctively widely ellipsoid to ellipsoid basidiospores and *G. ravenelii* and *G. zonatum* have oblong to cylindrical basidiospores. *Ganoderma* basidiospores have a cap in the apex (Figs. 6–7) that is obtuse and hyaline; after drying, the cap generally collapses and breaks, making the basidiospore apex truncate (Figs. 7–8). However, in some species where the cap is absent or very small, the basidiospores have a subacute apex, as in *G. atkinsonii*, *G. colossus*, *G. concinnum*, *G. dorsale*, *G. longistipitatum*, *G. oregonense,* and *G. perturbatum* (Figs. 9–11).

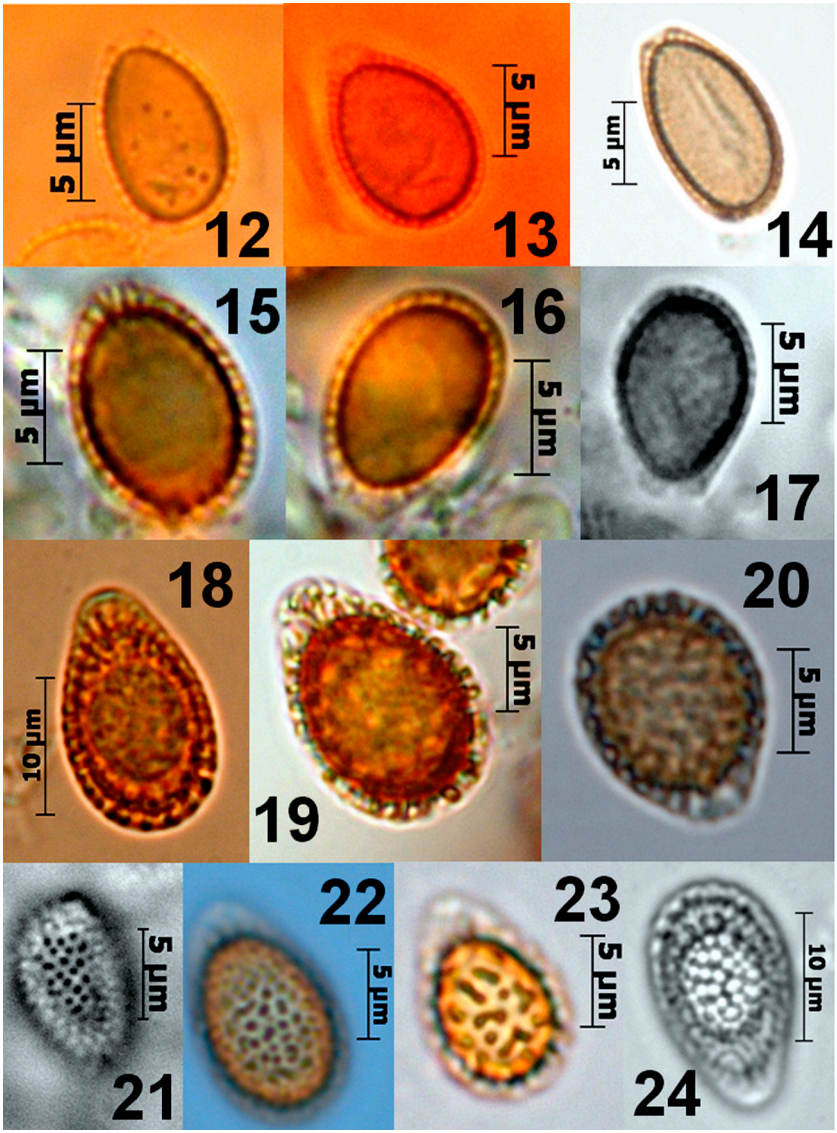
The basidiospore inter-walled pillars are thin to thick; thin (<0.3 μm) in *G. mexicanum*, *G. perzonatum*, *G. praelongum*, and *G. zonatum* (Figs.



Figs. 6–11. *Ganoderma* micromorphology. **6**. Basidiospores with cap *(G. multiplicatum)*. **7**. Basidiospore (right) with cap and (left) with truncate apex *(G. sessiliforme)*. **8**. Basidiospores with truncate apex *(G. chonoides)*. **9–11**. Basidiospores with subacute apex (9. *G. atkinsonii*; 10. *G. concinnum*; 11. *G. oregonense*).

12–14), intermediately thick (0.3–0.5 µm) in *G. corrugatum*, *G. curtisii*, *G. oerstedii*, *G. pulverulentum*, *G. resinaceum*, *G. sessiliforme*, *G. subincrustatum*, and *G. weberianum* (Figs. 15–17), and thick (0.5–0.7 µm) in *G. colossus*, *G. longistipitatum*, *G. oregonense*, and *G. perturbatum* (Figs. 18–20). The pillars can be free, sub-free, partially anastomosed, and reticulate (= anastomosed). "Free" pillars appear as dots on the basidiospore surface (e.g. *G. perzonatum*, fig. 21), while "sub-free" are free dots mixed with short anastomosed to shortly elongated structures (e.g. *G. elegantum*, fig. 22). "Partially anastomosed" is used when more than two pillars are grown together to form an irregular surface (e.g. *G. concinnum*, fig. 23), and "reticulate" is when the ornamentation forms an almost complete net (e.g. *G. colossus*, fig. 24).

Structure of the pilear cover. The pilear surface or pileipellis is formed by a cell layer similar to a hymeniderm, although in the majority of the species the cells do not originate from the same level as in the true hymeniderm. Clémençon (2004) defined the *Ganoderma* type of hymeniderm as a crustohymeniderm, which is characterized by thick-walled cells apically covered by a resinous



Figs. 12–24. *Ganoderma* micromorphology. **12–14**. Basidiospores with thin inter-walled pillars (12. *G. perzonatum*; 13. *G. praelongum*; 14. *G. zonatum*). **15–17**. Basidiospores with intermediate thick inter-walled pillars (15. *G. pulverulentum*; 16. *G. weberianum*; 17. *G. corrugatum*). **18–20**. Basidiospores with thick inter-walled pillars (18. *G. colossus*; 19. *G. longistipitatum*; 20. *G. perturbatum*). **21–25**. Disposition of the pillars in the basidiospores: 21. Free *(G. perzonatum)*; 22. Subfree *(G. elegantum)*; 23. Partially anastomosed *(G. concinnum)*; 24. Reticulate *(G. colossus)*.

matter. Cell sizes must be interpreted with care because they vary not only between species but also in the same specimen according to where the section has been made. Most species have club-like apical cells although there are species with branched or knobby cells besides the club shaped cells (Fig. 25).

The shape of the crustohymeniderm cells can be: (1) cylindrical (*G. perzonatum*), (2) almost cylindrical to narrowly clavate (*G. weberianum*), (3) widely clavate (*G. perturbatum*), and (4) clavate (most species). The cell wall is thick for all except *G. colossus*, where it is thin. A thick wall may be multi-stratified, related to the maturity state of the basidiomata; however, some species, like *G. perturbatum*, have an evidently multi-stratified wall. Some young pileipellis cells present secondary septa, more evident in the cells of the pileus periphery; furthermore, these peripheral cells tend to be lighter and shorter. Incrustations or granulations can also be present in the pileipellis. The incrustations are easily dissolved in KOH [e.g. *G. stipitatum*, fig. 27], while the granulations remain, because they are not alkali-soluble (e.g. *G. perzonatum*, fig. 26).

In some species the pileipellis cells have a transition from smooth club-like to antler-like cells. Protuberances and branches (as used in the descriptions below) differ in that "protuberances" are short projections or prolongations of the hyphal wall (generally≤ 8 μm long, located laterally or at the apex) that lack a lumen whereas "branches" may be short or large, apical or lateral but always possess a lumen. There are shape series in which the cell changes progressively, but a predominant shape is always observed (Fig. 25). Three large groups of crustohymeniderm cells might be found: entire (Figs. 25a, 26–28), lobulate-branched (Figs. 25b, 29–30), and branched (Fig. 31).

1) "Entire" crustohymeniderm cells are cylindrical, cylindrical with slightly wide apex, cylindrical to narrowly clavate, cylindrical with subcapitate apex, or narrowly clavate to widely clavate, generally lacking protuberances or branches, very occasionally with at most two, generally lateral protuberances, e.g. in *G. perturbatum*, *G. perzonatum*, *G. stipitatum*, and *G. sessiliforme* (Figs. 25a, 26–28).

2) "Lobulate-branched" crustohymeniderm cells may be subdivided into: a) clavate cells, with 1–3 round short thick protuberances and/or branches, but preserving the clavate shape (e.g., *G. nitidum*; *G. zonatum,* Fig. 25b); b) cells with no or 1-2 thick long branches and ≤ 7 short thick protuberances, where the clavate shape is generally lost (e.g., *G. oerstedii*; *G. subincrustatum,* Figs. 25c, 31; *G. multiplicatum,* Figs. 29–30).

3) "Branched" crustohymeniderm cells, with two types that generally lose the clavate shape: a) with 2-3 thin long branches with small protuberances (e.g., *G. orbiforme,* Fig. 25d) and b) the most striking, cells with many antler-like branches and small protuberances (e.g., *G. multicornum,* Fig. 25e).

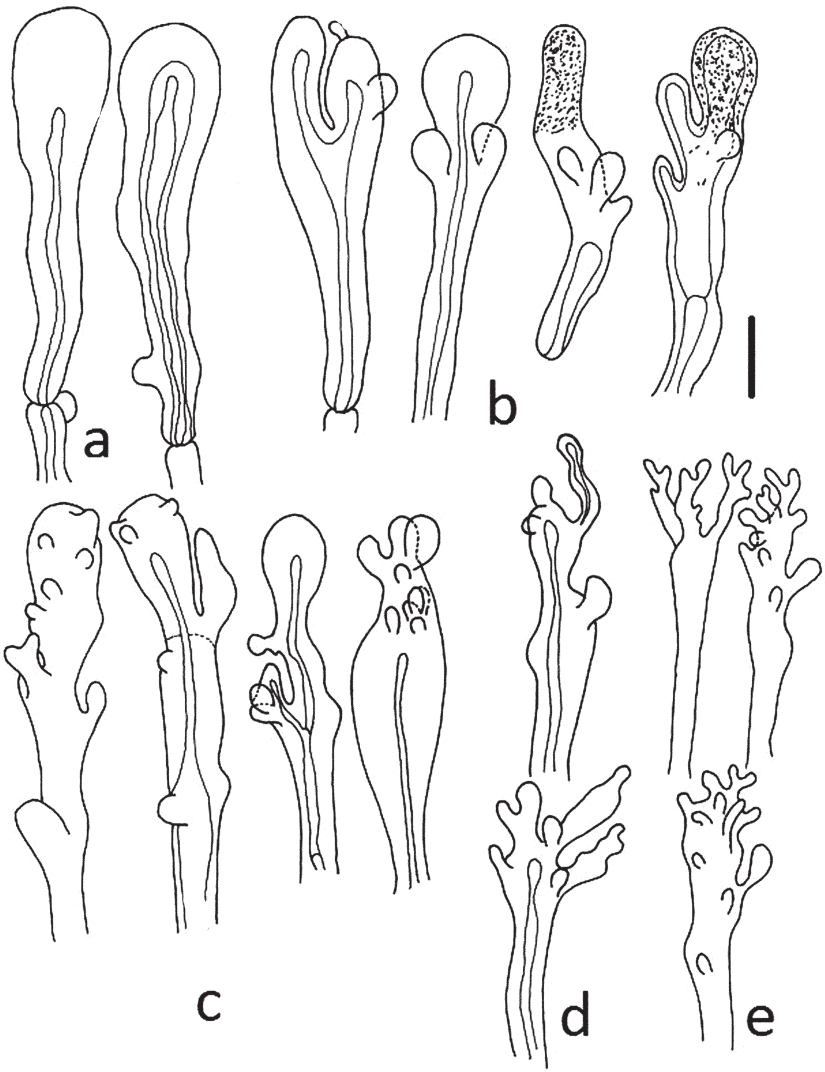


Fig. 25. *Ganoderma* crustohymeniderm cells. **a**. Entire *(G. perturbatum, G. sessile)*. **b**. Lobulate-branched *(G. nitidum, G. zonatum)*. **c**. Lobulate-branched with up to seven short and thick protuberances and 0 or 1–2 thick and long branches *(G. oerstedii, G. subincrustatum)*. **d**. Branched *(G. orbiforme)*. **e**. Antler-like *(G. multicornum)*.

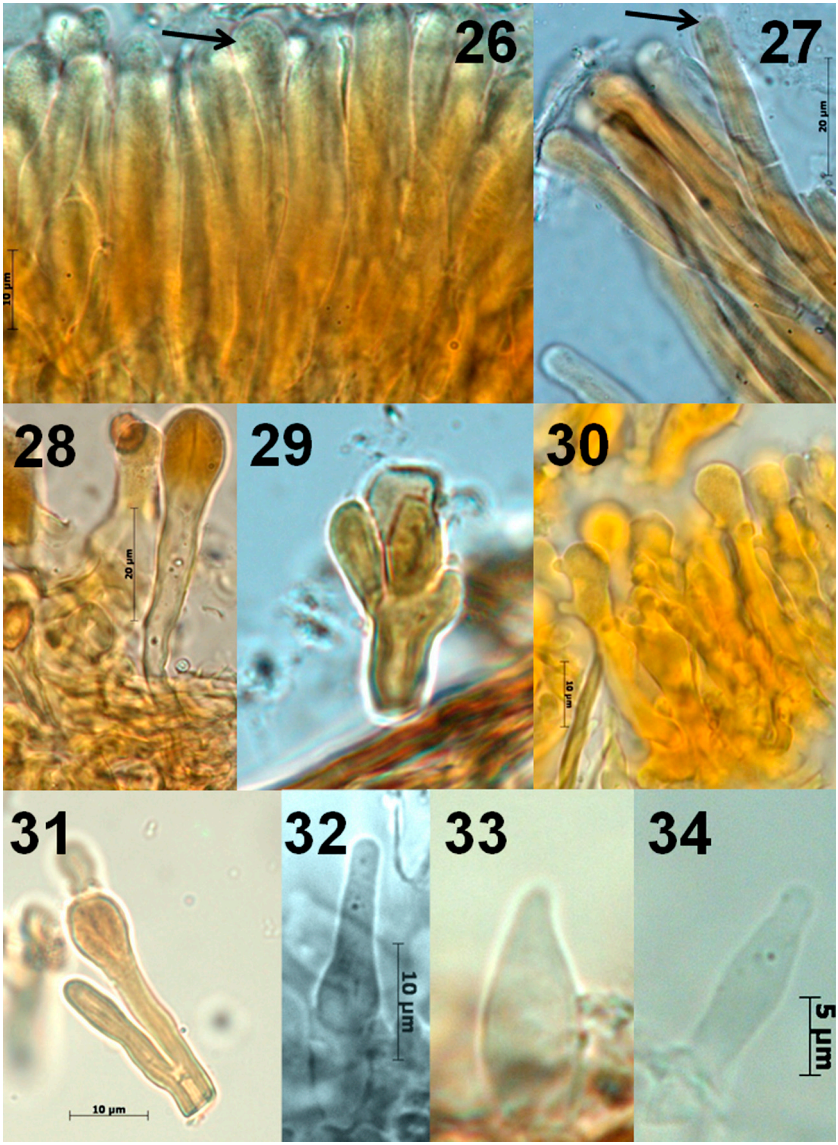
Hyphal system. In all species the hyphal system is di-trimitic, where generative and binding hyphae are generally difficult to observe. All generative hyphae have clamped septa and are hyaline to yellowish and (in almost all species) branched. Skeletal hyphae are of the arboriform type, thick-walled to solid, yellowish to yellowish-brown, apically branched; thin in the crustohymeniderm, wider in the context. Binding hyphae are generally thinner than skeletal hyphae, hyaline to yellowish-brown.

Cystidia. Vellinga (1998) defined them as sterile, differentiated, terminal elements in the hymenium. According with this definition *G. colossus*, *G. oregonense*, *G. perzonatum*, *G. pulverulentum*, *G. sequoiae*, and *G. stipitatum* have cystidia (Figs. 32–34), but they are difficult to observe.

Discussion

It is clear that species concepts vary in *Ganoderma* according to the author. Historically, *Ganoderma* taxa have been treated as species with great plasticity (e.g. *G. resinaceum* by Ryvarden, 2004) or (contrariwise) very narrowly (Steyaert 1972, 1980). Bazzalo & Wright (1982) and other authors, especially when synonymizing various different species under the same name, considered context color of little value. On the other hand, Steyaert (1967a) regarded the resin-like deposits as unimportant, mainly in the species of subg. *Elfvingia*. However, we found that these deposits together with context color are important in separating taxa. The resin-like deposit (termed "melanoid deposits" by Gottlieb & Wright, 1999 and melanoid substance by Steyaert, 1980) was called by Ryvarden (2000) "resinous bands," the term adopted here but more narrowly so as to differentiate actual resinous bands from more generalized resinous incrustations (small, fragmented deposits that do not form bands).

Ganoderma basidiospores have been traditionally described as double walled with a thin exosporium and thick endosporium, echinulate or with inter-walled pillars, or struts, or sinuous ridges, with truncate apex (Patouillard 1889, Murrill 1902, Haddow 1931, Overholts 1953, Corner 1983, Tham 1998, Ryvarden 2000, 2004 among others). The terms exosporium, episporium, and endosporium have been differently applied for the authors mentioned above if Clémençon (2004) is followed. Steyaert (1977) described the basidiospores with epi-endosporium and echinulate ecto-perisporium, sometimes the ecto-perisporium crestate besides echinulate. Bazzalo & Wright (1982), who used "perisporium" and "endosporium," considered the ornamentation as derived from the endosporium, in contrast to Clémençon (2004), who determined that the exosporium forms the ornamentation. As defined by Kirk et al. (2008), echinulate (diminutive of echinate: "having sharply pointed spines") does not apply to the inner ornamentation seen in *Ganoderma,* so we prefer to describe it as pillars. Bazzalo & Wright (1982) and Gottlieb & Wright (1999),



Figs. 26–34. *Ganoderma* crustohymeniderm cells (26–31): **26**. Cylindrical cells with granulations (arrow) of *G. perzonatum*. **27**. Cylindrical cells with incrustation (arrow) of *G. stipitatum*. **28**. Clavi-form cells without granulations of *G. sessiliforme*. **29**. Irregular cell with apical branches and protuberance of *G. multiplicatum*. **30**. Lobulate-branched cells with many protuberances of *G. oerstedii*. **31.** Lobulate-branched cell with a large lateral branch and a smaller apical branch of *G. multiplicatum*. **32–34**. Hymenial cystidia (32. *G. sequoiae*; 33. *G. perzonatum*; 34. *G. stipitatum*).

who observed the basidiospore pillars under SEM, proposed them as useful in determining species. We emphasize their usefulness by noting that not only are the pillars seen through SEM, pillar characters like size and disposition are also visible through light microscopy.

The basidiospore cap has been variously named: "bouchon perisporique" (Heim 1962), apical papilla (Furtado 1962), umbo (Corner 1983), and cap (Tham 1998). As mentioned above, when the cap collapses and breaks the basidiospore apex looks truncate; in few cases appears subacute, because the cap is very small or even absent. The term subacute, described by Steyaert (1972) for basidiospores with unchanged apex or apex unaltered at maturity, was adopted by Corner (1983), although this character has not been used systematically. We consider that it is an important feature in diagnosing taxa; for example, it supports *G. perturbatum* as independent from *G. resinaceum* and related to *G. dorsale*. *Ganoderma concinnum*, *G. dorsale*, *G. longistipitatum*, and *G. perturbatum* form a distinctive group of species by their stipitate basidiomata and subacute basidiospore apices.

Basidiospore shape is also an important diagnostic character. Oblong to cylindrical spores differentiate *G. ravenelii* and *G. zonatum* from morphologically similar species such as the ellipsoid spored *G. curtisii* and *G. orbiforme*.

Pileus surface is a complex structure in which the crustohymeniderm cells, hyphae and resinous-like substances are immersed. Many discussions on its taxonomic importance in *Ganoderma* have been made (e.g. Furtado 1965a, Gottlieb & Wright 1999, Steyaert 1980); however, its current use is limited, perhaps caused by a lack in precise terminology. Much of the complexity is caused by the great variability in the branching pattern of the cells in the same basidioma, creating confusion and difficulty to find a collective term. Torres-Torres & Guzmán-Dávalos (2005) realized that pileipellis cells vary greatly in size and shape depending on the site sampled and on the basidiome age. For this reason, tissues should be cut away from the basidiome edge, and only mature cells must be compared.

Imazeki (1939) and Steyaert (1980) classified genera based on pileipellis (dermis) type. Bazzalo & Wright (1982) had regarded pileipellis types described by preceding authors as valuable for identifying large groups but not useful for delimiting species. Subsequently, Gottlieb & Wright (1999) considered three general dermis types based partly on Steyaert (1980): a) "hymeniodermis *vera,*" b) "hymeniodermis formed by diverticulate hyphae… with similar endings, though wider through the apex, and with lateral branches, acanthophyses-like," and c) "hymeniodermis spheroid-pedunculate… composed of claviform filaments, with or without lateral diverticules, but always with emerging spheroid-pedunculate or capitate knobs at the apex." Their acceptance of these dermis types and basidiospore ornamentation as useful for delimiting taxa has

been confirmed in the present investigation. However, we found it difficult to assign species to one of these pileipellis types, we prefer to describe cells according to shape and the number of branches and protuberances. There is one species complex — *G. boninense*, *G. multiplicatum*, *G. orbiforme*, *G. subfornicatum* and *G. oerstedii*, all with yellowish-brown to reddish-brown context and pileipellis cells with protuberances and/or branches — in which species are differentiated base on basidiospore features and pileipellis cell shape and branch numbers.

Karsten (1881) did not mention cystidia in his original description of *Ganoderma,* and many mycologists accepted his non-cystidiate concept (Haddow 1931, Heim 1962, Furtado 1965b, 1967, Steyaert 1967b, 1972, Bazzalo & Wright 1982, Gilbertson & Ryvarden 1986, Ryvarden 1991, 2000). Although Corner (1983) noted that Demelius (1919) referred to acute 'cystidioles' in *G. applanatum* (Pers.) Pat. (subg. *Elfvingia*) and *G. lucidum* (Curtis) P. Karst., we follow Vellinga (1998) and regard them as true cystidia that are present in at least five species.

In conclusion, we consider that additional important features for characterizing *Ganoderma* species that can be directly observed or under light microscopy should include context color, structure, and resinous deposits; basidiospore pillar disposition and size; and pileipellis cell shape, protuberances, branches, and granulations.

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